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Food, Feeding, and Refuelling of Red Knots during Northward Migration at San Antonio Oeste, Rio Negro, Argentina (Alimentacion y Reabastecimiento de Playeros Rojizos *Calidris canutus rufa* Durante su migracion al Norte en San Antonio Oeste, Rio Negro, Argentina)

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FOOD, FEEDING, AND REFUELLING OF RED KNOTS DURING NORTHWARD MIGRATION AT SAN ANTONIO OESTE, RIO NEGRO, ARGENTINA

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Abstract.—We studied the food and feeding ecology of Red Knots *Calidris canutus rufa* on an area of rocky flat, or restinga, near San Antonio Oeste in the northwest of Golfo San Matías, Provincia de Río Negro, Argentina in March 1992. These Red Knots are on their way north, from “wintering” areas in Tierra del Fuego (Argentina and Chile) to the arctic breeding grounds in Canada. Three waves, each containing 5000–12,000 Knots, moved through the area. On the restinga they fed on banks of the small mussel *Brachidontes rodriguezi*, virtually the only prey taken. Variably sized (1–28 mm) *Brachidontes*, of which those between 5 and 20 mm were eaten (8–12 mm long mussels being positively selected), occurred in high biomass densities (23–117 g ash-free dry mass [AFDM]/m²). Due to its abundance, visibility, ease of detachment, slender shell form, and relatively weak shell, *Brachidontes* appear very suitable prey for Red Knots. Red Knots produced about 0.42 droppings/min. On the basis of a biomass equivalent of the droppings of approximately 62 mg AFDM, for conditions of balance (shell mass in = shell mass out) the intake rate was estimated at 0.433 mg AFDM/s. Making a few more assumptions, this translated into a net intake rate of 2.81 W, which would allow for a fat deposition rate of less than a gram of fat per day. Using more optimistic estimates of the various parameters in the energy budget model, a fat deposition rate of 5 g could be achieved. This is the order of magnitude predicted for Red Knots staging at San Antonio Oeste for 6–8 d and refuelling for the 1700 km long flight to the next known major staging area in southern Brazil.

ALIMENTACION Y REABASTECIMIENTO DE PLAYEROS ROJIZOS *CALIDRIS CANUTUS RUFUS* DURANTE SU MIGRACION AL NORTE EN SAN ANTONIO OESTE, RIO NEGRO, ARGENTINA

Sinopsis.—Se estudiaron la dieta y la ecología alimentaria de los Playeros rojizos *Calidris canutus rufa* en un área de restinga cercana a la localidad de San Antonio Oeste en el noroeste del Golfo San Matías, Provincia de Río Negro, Argentina, durante marzo de 1992. Estos Playeros rojizos que estaban migrando al norte, provenían de sus zonas de “invernada” en Tierra del Fuego (Argentina y Chile) y se dirigían a sus áreas reproductivas en el Polo Norte canadiense. Tres pulsos de 5.000 a 12.000 Playeros se movieron a través del sitio. Todos se alimentaron sobre manchones de mejillines *Brachidontes rodriguezi*, prácticamente la única presa ingerida. La densidad de la biomasa de *Brachidontes* fue muy alta (23–117 g de Masa Seca Libre de Cenizas/m²) y distribuida en tallas variables (1–28 mm), pero sólo fueron ingeridas las comprendidas entre 5 y 20 mm de largo (seleccionándose positivamente los mejillines de 8–12 mm de largo). *Brachidontes* parece ser una presa muy conveniente para

los Playeros rojizos por su abundancia, visibilidad, facilidad de despegue, forma estrecha y baja resistencia de las valvas. Los Playeros produjeron alrededor de 0,42 heces/min. Considerando que la biomasa equivalente de las heces es aproximadamente 62 mg MSLC, para las condiciones de equilibrio (masa de las valvas ingeridas = masa de las valvas defecadas), la tasa de ingestión fue estimada en 0,433 mg MSLC/s. Haciendo unas pocas asunciones esto puede trasladarse a una tasa neta de ingestión de 2,81 Watt que podría permitir una tasa de deposición de grasa de menos de un gramo por día. Utilizando estimaciones más optimistas (y no necesariamente menos realistas) de varios parámetros del modelo de presupuesto de energía, podría alcanzarse una tasa de 5 g de deposición de grasa por día. Este es el orden de magnitud predicho para los Playeros rojizos que permanecen a San Antonio Oeste reabasteciéndose durante 6–8 días para volar 1700 km de distancia hasta la siguiente gran área de estadía en el sur de Brasil.

Red Knots (*Calidris canutus*) are spectacular long-distance migrant shorebirds that breed in high arctic tundra and spend the nonbreeding season much farther south in temperate and tropical coastal areas (Morrison 1983, Piersma and Davidson 1992). The southernmost nonbreeding areas occupied by Red Knots are those of the subspecies *C. c. rufa*, at 54°S in Tierra del Fuego (Harrington 1982, 1983, 1986, 1996; Harrington and Morrison 1980; Morrison and Ross 1989). These Red Knots breed 15,000 km farther north, in the Canadian Arctic (Morrison and Harrington 1992) and make one of the longest nonstop flights known in the avian world (possibly up to 8000 km). Compared to the other subspecies of Red Knots, *rufa* undertakes the longest overall migration between breeding and nonbreeding areas, has a relatively small population size, and is ecologically rather little known (Piersma and Davidson 1992, see popular account by Harrington 1996).

Red Knots of the *rufa* subspecies begin their northward migration in mid-February. Red Knots were observed on passage in Argentina at Península Valdés (Morrison and Harrington 1992), coastal sites in Buenos Aires Province (Myers and Myers 1979), Punta Rasa (Blanco et al. 1992), and Bahía Samborombón (Vila et al. 1994). Farther north, small numbers of passage birds are seen in the north of Uruguay (Vaz-Ferreira 1961) and in southernmost Brazil (Harrington et al. 1986). Only recently has the importance of the region of San Antonio Oeste, in the northwest corner of Golfo San Matías, been recognized (González 1991). These combined observations suggest that between San Antonio Oeste and southern Brazil no coastal areas exist that harbour more than a few thousand Red Knots during northward migration.

There are no published studies on the food and feeding of Red Knots in South America, but there is a wealth of comparative knowledge from other subspecies spending the nonbreeding season in coastal areas in Europe, Africa, and Australasia (e.g., Alerstam et al. 1992; Moreira 1994; Piersma 1991; Piersma et al. 1993a,b, 1994, 1995; Prater 1972; Tulp and De Goeij 1994; Zwarts and Blomert 1992; Zwarts et al. 1992). Indeed, there exists little published knowledge on the feeding and intertidal food resources of any of the many migratory shorebird species along the shores of South America (but see Navarro et al. 1989, Swennen et al. 1982, Velásquez and Navarro 1993). In this contribution we describe the feed-

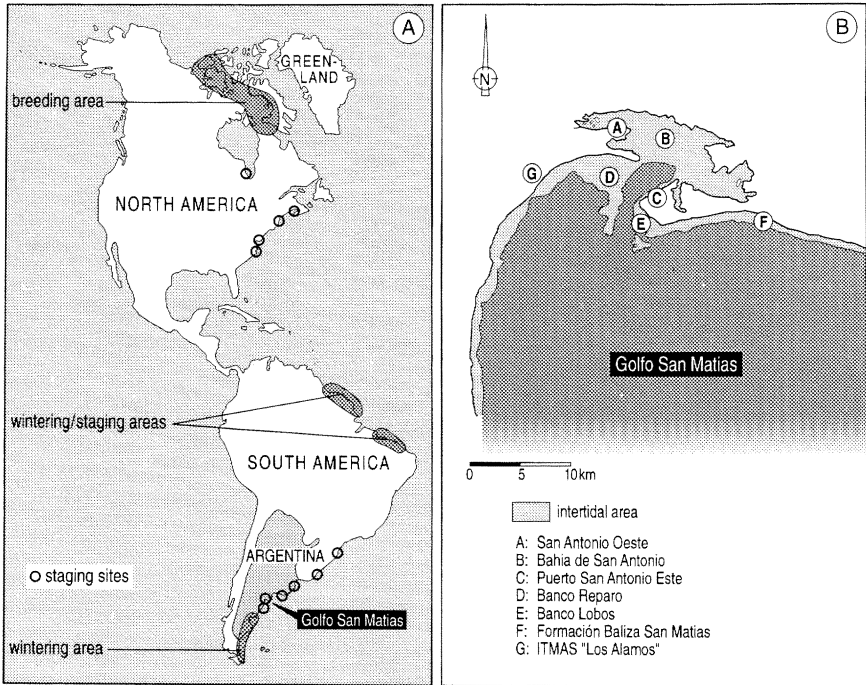


FIGURE 1. Summary of the breeding, staging and wintering areas of *Calidris canutus rufa* (A), and of the study areas at San Antonio Oeste, Río Negro, Argentina (B).

ing behavior, food choice, intake rate, and possible refuelling rates that can be achieved, of northward migrating Red Knots at a staging area in Golfo San Matías, Argentina, and present data on the food stocks. Such knowledge will help us to understand the migration strategies of this spectacular long-distance migrant, which in turn may help to provide biological arguments for safeguarding the coastal habitats on which they rely.

STUDY AREA

In the region of San Antonio Oeste (Fig. 1), Red Knots use three different types of intertidal habitats. Most important were the rocky flats or *restinga* near the Instituto Técnico Minero y de Aguas Subterráneas (ITMAS) "Los Alamos" and at the Formación Baliza San Matías (Fig. 1). Restinga was described by Murphy (1936, quoted by Harrington & Morrison [1980]) as "a broad wave-cut platform in the country rock . . . between tides but nearer low tide . . . its surface broadly plane, but very rough in detail, with many pools in which fishes and other marine animals survive between tides . . . the rocky projections are usually covered with mussels." In addition, the sand banks at Banco Reparo and Banco Lobos, and the beaches between Banco Lobos and Baliza San Matías were used by Red Knots (González 1991).

This study was carried out on the restinga along the shores near Los Alamos, 12 km south of San Antonio Oeste ($40^{\circ}46'S$, $65^{\circ}02'W$). Our study area stretched from Los Alamos 700 m along the coastline to the southwest. Here, Red Knots and other shorebirds commute 100–1800 m between the low tide feeding areas on the restinga, and the high tide roosts on the adjacent beach. The width of the restinga between the low water and the high water line varies between 500–800 m. The tidal regime is semidiurnal and the tidal amplitude varies between 6.5 m at neap, and 9.3 m at spring tides. The restinga has a total length of 9 km. The siltstone of which the restinga consists has a flat surface, and is dotted with holes up to 40-cm deep, sometimes with accumulations of sand and silt. Large parts of restinga, especially those halfway between the high and the low water lines, are covered with mussels.

The climate in San Antonio Oeste is influenced by strong westerly winds and the subtropical anticyclones of the south Atlantic. Over the period 1990–1994, annual rainfall averaged 310 mm and mean annual air temperature averaged 11.7 C. In March the average maximum air temperature was 24.1 C, with an overall average of 15.8 C and a mean daily range of 12.1 C. Rainfall in March averaged 48 mm (Punta Delgada Station; Departamento Provincial de Aguas 1995).

Red Knots share the area with other species of shorebirds, mostly White-rumped Sandpipers (*Calidris fuscicollis*), Sanderlings (*Calidris alba*), and Two-banded Plovers (*Charadrius falklandicus*). Raptors that may prey on shorebirds are only rarely observed. The study area is frequented by tourists and fishermen, who are much more common in January and February (the peak holiday season) than in March. The most frequent disturbances are due to the movements of vehicles and persons during high tide, leading to regular displacements of the roosting birds. The shoreline at Los Alamos is part of the recently created Provincial Protected Natural Area “Bahía de San Antonio.” In August 1993, this area was recognized as an “international site” by the Western Hemisphere Shorebird Reserve Network.

METHODS

This study was carried out on 13 days between 1–28 Mar. 1992. On five occasions Red Knots were continuously followed from high water to low water. On eight occasions the birds were studied during part of the diurnal tidal cycle only. Additional observations on defecation rates of Red Knots were collected in February–March 1993. Mussel samples to measure breaking forces were collected in March 1995. During all observations, binoculars (10×40 and 16×50) and a zoom-telescope ($15\text{--}45\times$) were used.

After flocks had moved from their feeding areas, samples of 20–30 droppings were collected from three spots with surface areas of respectively 4×50 m (A), 4×25 m (B), and 4.5×18.5 m (C) (see Fig. 4). The fecal pellets were dried and analysed according to the methods outlined by Dekinga and Piersma (1993). After sieving the dried feces over

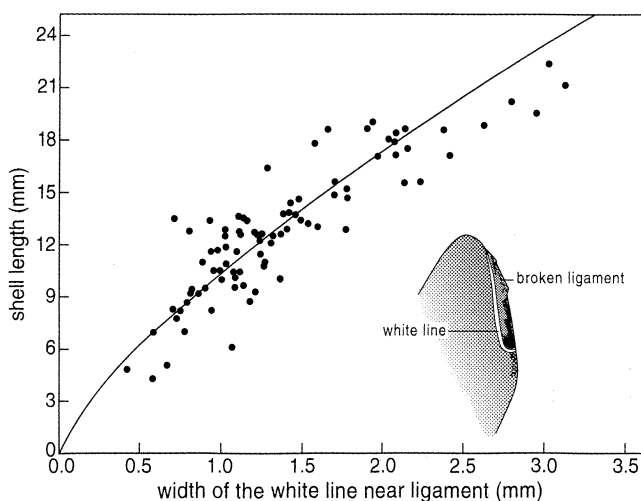


FIGURE 2. Shell length of *Brachidontes rodriguezii* as a function of the width of the white line near the ligament. The double-logarithmic regression line shown is represented by the following equation: $y = 10.34 \times x^{0.744}$, $r^2 = 0.80$, $n = 98$. The inset showing the interior of *Brachidontes* indicates the white line of which the width was taken.

a 0.3-mm mesh, the shell material was examined under a binocular microscope. The shell mass remaining on the 0.3 mm sieve was weighed to the nearest 0.1 g. We estimated sizes of ingested mussels (*Brachidontes rodriguezii*) by measuring (nearest 0.1 mm) the widths of the white areas bordering the ligaments on recognizable shell fragments. Maximum shell length was a double-logarithmic function of this dimension (Fig. 2).

Densities and biomass of mussels were estimated for the three areas where droppings had been collected. On two of these, three complete patches covered with mussels were collected and analysed. The surface areas were measured with transparent mm-paper; they measured 0.0071, 0.0043, and 0.0036 m² at A and 0.0079, 0.0071 and 0.0050 m² at B. On the third site (C), 10 samples of 0.006 m² each were taken with a circular metal corer. Coverage by mussels was estimated visually at the sampling locations, except for the third one, where the estimation was made by measuring the distance between the mussel patches. The samples were sieved over a 1-mm mesh and dried at 50–60 °C. Then the mussels were sorted according to shell length to the nearest mm. Samples of mussels without crusts of barnacles were weighed and incinerated for 5 h at 550 °C to determine the ash mass (ASH), and, with subtraction from dry mass, ash-free dry mass (AFDM). The ratio AFDM/ASH was calculated for each length class. This ratio is needed to predict the biomass equivalent of droppings on the basis of fecal shell mass (which is approximately equal to [0.977×] ingested ash mass; Dekinga and Piersma 1993).

To describe whether particular size classes of mussels were preferred, we used Ivlev's electivity index *E* (Jacobs 1974), which is defined as $E =$

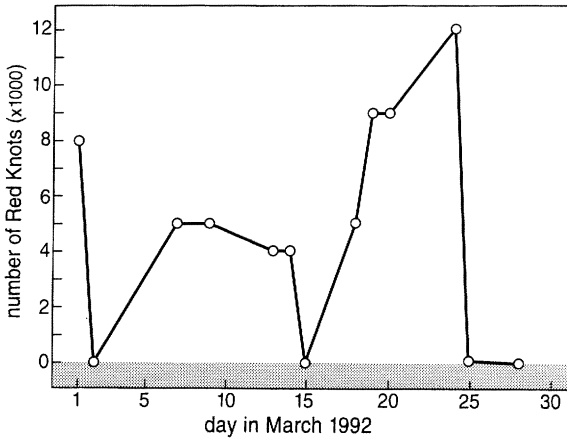


FIGURE 3. Total number of Red Knots observed at the study area near San Antonio Oeste in March 1992.

$(r - p)/(r + p)$ where r = fraction of a certain size class taken by the Red Knots and p = fraction of that size class present in the mussel population. Positive values of E indicate a preference, negative values an underrepresentation in the diet. To test for statistical significance of selection or rejection (over 2-mm size categories) we used contingency analyses in which the adjusted residuals of observed and expected frequencies were computed and tested against a t -distribution (Everitt 1977:46–48). We assumed that selection or rejection was significant at $P < 0.05$.

To calculate a value of defecation rate, a small area of restinga (10–30 m²) was selected where the tide had just receded and no birds could have left their droppings, but where feeding Red Knots were expected to come with the incoming tide. The areas also had to be visually sufficiently distinct from the surrounding restinga. By recording the number of Red Knots feeding on such an area over a certain time interval (noting the number every time that it showed a change), the number of bird-minutes spent there could be calculated. After the birds had left, the number of deposited droppings was counted. Defecation rates (droppings/bird-min) were calculated as the number of droppings divided by the number of bird-min.

RESULTS

Occurrence of Red Knots.—The number of Red Knots present in the study area in March varied from 0–12,000 birds (Fig. 3). On the basis of simultaneous observations (by other observers) at other sites in the region than Los Alamos, we are confident that days without Red Knots at the study site represent real absences from the San Antonio Oeste area. This indicates that birds stay in the area for short periods only, the latter two waves visible in Figure 3 suggesting staging times of 6–8 d. If the

TABLE 1. Density (number/m²) and biomass (g AFDM/m²) of mussels *Brachidontes rodriguezi* on three different areas of restinga at Los Alamos near San Antonio Oeste in March 1992 where droppings of Red Knots were collected as well (Fig. 4). Sampling sites are indicated by date of sampling and the distance between the sampling site and the high tide line. Two density and biomass values are presented: those referring to all mussels, and those referring to the mussels of the ingested size classes only (5–20 mm long, Fig. 4). Note that the “400-m sites” of 1 and 9 March are not the same.

| Date | 1 March | 1 March | 9 March |
|-----------------------------|-----------|-----------|-----------|
| Site: distance from HW line | 100 m (A) | 400 m (B) | 400 m (C) |
| Area covered by mussels (%) | 7.7% | 10% | 38.5% |
| Density all sizes | 1792 | 2488 | 5990 |
| Density selected sizes | 1438 | 1491 | 4670 |
| Biomass all sizes | 23.1 | 31.2 | 117.4 |
| Biomass selected sizes | 21.6 | 22.1 | 75.5 |

three peaks in numbers represent separate waves of northward migrating birds, the total number of Red Knots using the study area was close to 25,000 birds. With a total population of 125,000 (Morrison and Harrington 1992), no less than 20% of the world population of *C. c. rufa* staged at San Antonio Oeste in March 1992.

Feeding behavior and activity.—During high tide the Red Knots roosted on the beach in one or more dense flocks. They dispersed in groups of several hundred birds over the restinga as soon as the intertidal area became available during the receding tide, usually following the water line. Walking in parallel and facing the wind, feeding Red Knots made repeated “probes” with their bills (though not in a vertical, sewing, manner as on soft sediments; see Piersma et al. 1995, Zwarts et al. 1992) in the edges of clumps of mussels, thus trying to identify single mussels that could be detached. Detached mussels were not washed before ingestion. Handling times were short, at most 1–2 s.

Food abundance.—The musselbeds consisted almost exclusively of *Brachidontes rodriguezi*. A few individuals of other molluscs, and of polychaete and amphipod species were encountered, but these items accounted for a maximum of one percent of the biomass present. Total densities of *Brachidontes* varied from 1800–6000 individuals per m² (Table 1). Of these, 60–80% were of the appropriate sizes for ingestion by Red Knots (5–20 mm; Fig. 5).

To convert the size frequency and density estimates of *Brachidontes* into biomass, we require information on the shell size-biomass relationship (Fig. 4A). On the basis of this function and the size distribution presented in Figure 5, total biomass of *Brachidontes* varied in parallel with total mussel densities, ranging from 23–117 g AFDM/m² for all size classes, and from 21.6–75.5 g AFDM/m² for ingested size classes only (Table 1).

Diet and size selection.—The droppings of Red Knots consisted entirely of shell fragments of *Brachidontes*. A search through the fragments retained on the 0.3-mm sieve of three samples of a total of 90 droppings, yielded 192 measurable fragments from which the size distribution of

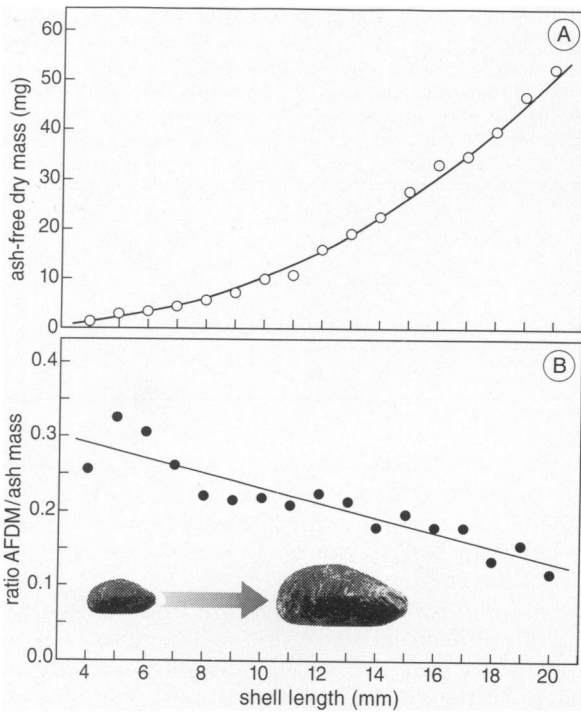


FIGURE 4. Ash-free dry mass (AFDM) (A), and the ratio of AFDM and ash mass (B), as functions of shell length (SL) in *Brachidontes rodriguezi* from San Antonio Oeste in March. The regression line shown in A is based on $AFDM = 0.0506 \cdot SL^{2.312}$, $r^2 = 0.996$, $n = 17$. The regression line in B is based on $AFDM/ash = 0.329 - 0.0098 \cdot SL$, $r^2 = 0.83$, $n = 17$. The relationship between ash mass and SL (not shown), was best described by $ash = 0.0791 \cdot SL^{2.791}$, $r^2 = 0.989$, $n = 17$.

ingested *Brachidontes* could be reconstructed (Fig. 5). Although there was a wide range of size classes available (1–28 mm, Fig. 5), Red Knots only ate *Brachidontes* with lengths between 5–20 mm. On all three occasions, the size distribution of ingested *Brachidontes* differed from the size distribution of those available (Chi-squared tests, $P < 0.0001$). The average length of all ingested *Brachidontes* was 10.3 mm. Red Knots did not eat the smallest and the largest mussels present on the restinga (Fig. 5).

Although a comparison of ingested and present size distributions of *Brachidontes* tells us about the size classes that are avoided, it does not tell whether there are sizes that are actively selected or taken in smaller number than present. For the samples on 1 March, *Brachidontes* measuring 8–11 mm were significantly positively selected, whereas those <5 mm and >16 mm were taken significantly less than expected ($P < 0.05$) (Fig. 6). For the samples on 9 March, mussels between 10–12 mm were significantly positively selected, and those <5 mm and >18 mm were rejected.

Biomass equivalents of droppings, defecation rate, and estimated intake

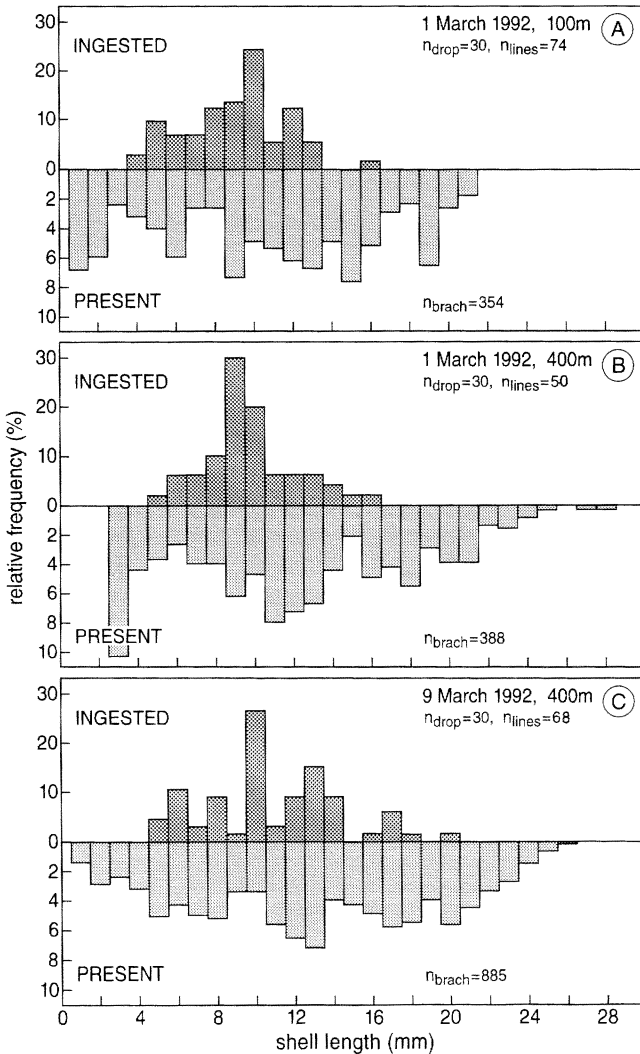


FIGURE 5. Size distributions of *Brachidontes rodriguezii* ingested by Red Knots on three occasions (upward histograms) in comparison with the size distributions of *Brachidontes* present on the respective feeding sites (downward histograms). For each occasion the date and the distance perpendicular downshore of the high water line are given.

rate.—The mass of shell fragments retained on a 0.3 mm sieve for the three samples of 30 droppings analyzed in detail in Figs. 5 and 6, were 6.96, 9.31, and 8.77 g respectively, with an average of 8.35 g, or 0.278 g/dropping. This rather high value (cf. Dekinga and Piersma 1993:fig. 8) can be recalculated as ash mass per dropping by multiplying by a factor of 0.977 (=0.272 g). To estimate the average biomass-equivalent of these

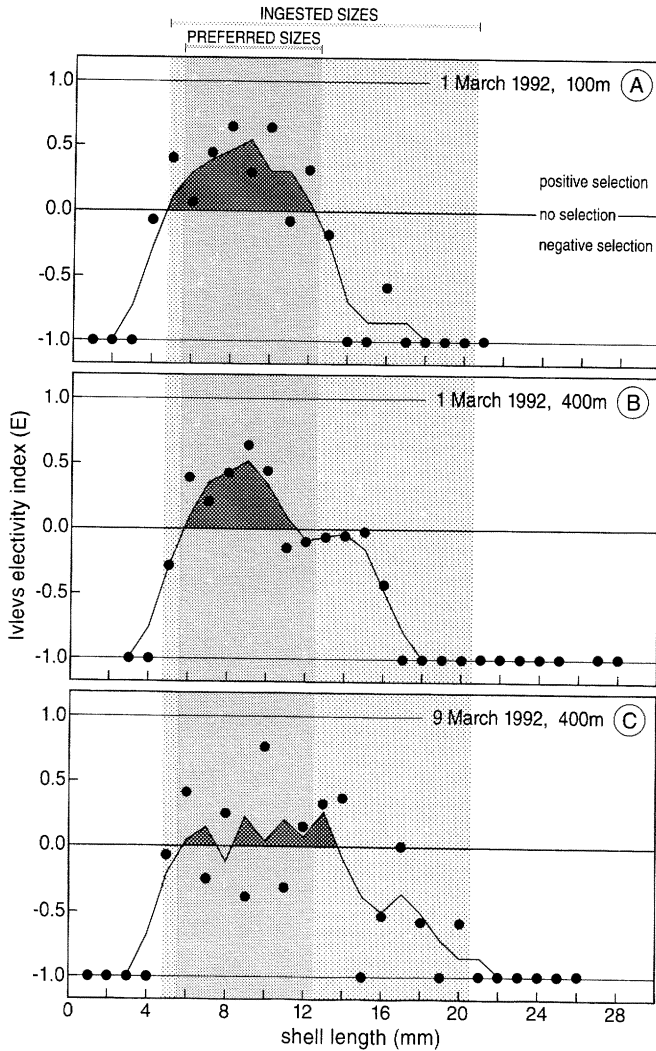


FIGURE 6. Size selection of *Brachidontes rodriguezii* by Red Knots based on the ingested and present size distributions given in Figure 5. Size selection is indicated by Ivlev's electivity index E, where the zero line indicates no selection, positive figures indicate positive selection, and numbers below zero indicate negative selection. The lines are three-point running means.

droppings, we multiplied the estimated ash mass by the appropriate ratio of AFDM and ash mass, which is a negative function of shell length (Fig. 4B). Given an average ingested shell length of 10.3 mm and assuming a normal distribution of ingested shell lengths, this ratio was 0.228, yielding a biomass-equivalent per dropping of $0.272 \cdot 0.228 = 0.062$ g AFDM. To

TABLE 2. Four measurements of defecation rate based on timed observations of Red Knots on recognizable areas of restinga and counts of the droppings they have produced during this time. All data collected in 1993.

| Date | Number of birds | Time (min) | Bird-min | Number of droppings | Defecation rate (droppings/bird-min) |
|-------------|-----------------|------------|----------|---------------------|--------------------------------------|
| 27 February | 46 | 32.0 | 1472 | 485 | 0.33 |
| 23 March | 84 | 98.0 | 8232 | 2672 | 0.32 |
| 25 March | 20 | 13.2 | 264 | 138 | 0.52 |
| 27 March | 104 | 5.0 | 520 | 264 | 0.51 |

obtain an estimate of intake rate, we assumed conditions of balance (shell mass in = shell mass out), so that we could multiply this factor by the defecation rate of Red Knots. Defecation rate of Red Knots feeding on *Brachidontes* on the restinga of Los Alamos varied from 0.32–0.52 droppings/bird-min. The average was 0.42 droppings/bird-min (Table 2). The intake rate would thus be estimated as $0.062 \cdot 0.42 = 0.026$ g AFDM/min, which translates into 0.433 mg AFDM/s.

DISCUSSION

Diet choice.—The diet of Red Knots on the restinga at San Antonio Oeste appears to consist of the dominant local mussel species, *Brachidontes rodriguezi*. This first documentation of the diet of Red Knots feeding on rocky flats confirms the brief description by Harrington and Morrison (1980). Red Knots foraging on soft sediments elsewhere may eat mussels as well (in such cases the related mussel species *Mytilus edulis*; Piersma et al. 1993b, Zwarts and Blomert 1992), but *Mytilus* is not usually the preferred prey species because there are better alternative items (i.e., prey with a bigger meat content relative to shell mass and strength, Zwarts and Blomert 1992). To examine whether the predominance of *Brachidontes* in the Red Knots' diet is a consequence of the absence of alternative prey, we have to examine size selection in a broader context. Like many *Mytilus* on western European intertidal flats, *Brachidontes* appears a suitable prey because it is highly visible in good densities, and because it is distributed in relatively small clumps that provide much "edge" from which birds can detach individual mussels. *Brachidontes*, much more than *Mytilus edulis* on musselbanks in western Europe and in Tierra del Fuego, Argentina, appear easy to pull off the substrate (pers. obs.). *Brachidontes* are slender, with a low width to length ratio (Fig. 4). Their circumference of about 30 mm, the threshold above which Red Knots are unable to swallow their hard-shelled prey (Piersma 1991, Zwarts and Blomert 1992), is not a factor to be considered since even a 25-mm-long *Brachidontes* has a perimeter of only 33 mm.

Earlier studies (Piersma et al. 1993c) had indicated that Red Knots were able to crack, in their muscular gizzard, shells of *Mytilus edulis* up to a

breaking force of 0.4 N. A further comparison with two additional mussel species from the Chilean rocky intertidal zone fed upon by Surfbirds *Aphriza virgata* (a similar-sized mollusc-eating close relative of Red Knots; Jehl 1968, Piersma 1994), shows that the upper limit of ingested size classes also corresponded to breaking forces of about 0.4 N (Navarro et al. 1989; R. A. Navarro, pers. comm.). We measured the force required to break the shell of *Brachidontes*, and found that the mussels <20 mm required considerable less force to break than 0.4 N. Although small *Brachidontes* were harder to break than small *Mytilus*, large *Brachidontes* were quite easy to crack.

Overall, *Brachidontes* seems to provide suitable prey for Red Knots. The mussels are abundant and easily detectable, easy to detach from the substrate and easy to crush in the gizzard. In the absence of detailed data on handling times, we can not calculate profitability as a function of shell length in order to compare the suitability of *Brachidontes* relative to the buried tellinid bivalve *Macoma balthica*, the preferred prey of Red Knots in the Wadden Sea (Piersma et al. 1994, Zwartz and Blomert 1992).

There are many questions that remain. As is true for other areas where the feeding of Red Knots has been studied, we do not know the mechanism of size selection on the restinga at San Antonio Oeste. Is it a visible mechanism based on experience (note the obvious size difference between a small and a large *Brachidontes* illustrated in Fig. 4)? Is it the result of a tendency for 6–12 mm long mussels occurring along the edge of clumps? Or is it the outcome of birds randomly pulling at shells in clumps, with those measuring 8–12 mm long being easiest to detach? In other words, is the size selection (Fig. 6) the outcome of an active behavioral process on the part of the birds, or a passive process effected by the availability characteristics of the prey (Hulscher 1982)? A deeper understanding of size selection might suggest explanations for the observation that at San Antonio Oeste some parts of the restinga with abundant *Brachidontes* are intensively used by Red Knots, while apparently similar nearby areas are not used at all (P. M. González, unpubl. obs.).

Biomass equivalents and dropping rates.—Some authors have reconstructed biomass equivalents on the basis of the AFDM of the meat only (AFDM_{meat}), whereas others used the total AFDM in shell and meat (AFDM_{total}). For wintering Red Knots in New Zealand, Piersma (1991) estimated biomass equivalents of 8.3–15.3 mg AFDM_{total}/dropping. Dekinga and Piersma (1993) came up with an average estimate of 29 mg AFDM_{meat}/dropping for Red Knots feeding on *Macoma balthica* in the Wadden Sea in September, and of 38 mg AFDM_{total}/dropping for birds feeding on a species of mudsnail (*Hydrobia ulvae*) in October. Northward migrating Red Knots in the Wadden Sea (Piersma et al. 1994:table 1) are reported to show average biomass equivalents of 25.24 mg AFDM_{meat}/dropping (range 5.98–51.81, $n = 12$) when predominantly eating *Macoma*, 15.07 mg AFDM_{total}/dropping when feeding mainly on *Hydrobia* (range 8.2–23.25, $n = 6$), and 16.49 mg AFDM/dropping when feeding on an evenly mixed diet (range 7.86–24.75, $n = 6$). Our estimate

of 62 mg AFDM_{total}/dropping lies firmly in the upper part of the distribution. This is even so with respect to those referring to AFDM_{meat}/dropping; taking into account that about 40% of the biomass of mussels resides in the chitinous layers of the shell (data from *Mytilus edulis*, J. Samuels and T. Piersma, unpubl. data), this would give a biomass equivalent of 37.2 mg AFDM_{meat}/dropping. We must conclude that northward migrating Red Knots in the San Antonio Oeste region produce relatively large droppings.

There are two published estimates of defecation rates. Alerstam et al. (1992), studying northward migrating Red Knots in Iceland, followed individual birds with binoculars and telescopes for a total of 407 min. They recorded 0.27 droppings/bird-min. (A similar estimate of 0.26 droppings/bird-min was published for spring staging Great Knots *Calidris tenuirostris* in northwest Australia by Tulp and De Goeij 1994.) Using the same technique, Zwarts and Blomert (1992) estimated the mean dropping interval of a single Red Knot during southward migration in the Wadden Sea over 21 min of continuous observation as 80 s. This equals 0.75 droppings/bird-min. Our estimates based on counts of droppings on small delineated areas of which the use in bird-min was estimated, are comfortably between these values: 0.33–0.52 droppings/bird-min (Table 2), with an average of 0.42 droppings/bird-min. The existence of digestive strategies for optimally processing ingested food could result in defecation rates varying adaptively in different ecological conditions (see Prop and Vulink 1992). For now, the comparative data set is too limited to examine this hypothesis in Red Knots.

Estimates of intake and refuelling rates.—A few attempts have been made to construct energy budgets for northward migrating Red Knots (Alerstam et al. 1992, Piersma et al. 1994). These attempts have in common the finding that energy gains during refuelling can not, or can only just, be accounted for. On the basis of our data we have made a similar attempt, including a sensitivity analysis based on multiplications (and additions) of all the lowest and highest parameter values (Table 3; this table also gives all the details, our assumptions and the references to literature). On the basis of the averages, Red Knots staging on restinga at San Antonio Oeste would be able to store slightly less than 0.5 g of fat per day (note that not all body mass gain is necessarily fat, Lindström and Piersma 1993). For the scenario with the lowest parameter values, staging birds would lose a few g/d, and according to the most optimistic scenario the birds would gain no less than 5 g fat/d. Maximum average body mass increases of Red Knots at refuelling sites during northward migration are in the order of 3–4 g/d (e.g., Davidson and Wilson 1992, Piersma et al. 1992, Wilson and Morrison 1992), values which also hold for individual birds (T. Piersma, unpubl. data).

Six Red Knots captured on the study site on 27 Mar. 1993, in the middle or near the end of a migration “wave,” had an average mass of 139 g (range 114–152.5 g, P. Y. Bergkamp, pers. comm.), but no information on mass gains during their stopover is available. The flight of 1700 km to

TABLE 3. Energy budget estimates of Red Knots refuelling during northward migration in Golfo San Matías, Argentina. A budget based on the average values given in the text or literature is provided in the second column; a sensitivity analysis based on the lowest or highest likely value is given in the third and the fourth columns. All variables are expressed in seconds and in Watts (i.e., J/s).

| Variables | Mean estimate | Lowest estimate | Highest estimate |
|---|---------------|-----------------|------------------|
| Average daily intake | | | |
| Defecation rate (droppings/s) | 0.0070 | 0.0053 | 0.0085 |
| Biomass equivalent (mg AFDM _{total} /dropping) | 62 | 52 | 71 |
| Intake rate during foraging (mg AFDM _{total} /s) | 0.433 | 0.276 | 0.640 |
| Feeding period (s) ^a | 46,800 | 43,200 | 50,400 |
| Overall intake rate (mg AFDM _{total} /s) | 0.235 | 0.138 | 0.352 |
| Energy equivalent (J/mg AFDM _{total}) ^b | 21 | 20 | 22 |
| Gross intake rate (W) | 4.94 | 2.76 | 7.74 |
| Assimilation efficiency (fraction of gross intake) ^c | 0.57 | 0.50 | 0.64 |
| Net intake rate (W) | 2.81 | 1.38 | 4.96 |
| Average daily expenditure | | | |
| Basal metabolic rate (W) ^d | 1.1 | 1.3 | 0.9 |
| Cost of activity (W) ^e | 1.5 | 1.7 | 1.3 |
| Total rate of energy expenditure (W) ^f | 2.6 | 3.0 | 2.2 |
| Daily balance | | | |
| Rate of energy gain/loss (W) | +0.21 | -1.62 | +2.76 |
| Daily fat storage or loss (g/day) ^g | +0.39 | -3.52 | +5.11 |

^a Based on 12–14 h of 100% feeding activity during low water periods at day and night (P.M. González, unpubl. data).

^b Unpublished data of J. Samuels and T. Piersma based on adiabatic bomb calorimetry of AFDM_{total}.

^c Based on Piersma (1994: 53):table 3 for digestive efficiency (on the basis of AFDM_{total} of Red Knots eating *Mytilus edulis*).

^d Based on measurements of Piersma et al. (1996), and the assumption of no maintenance costs at an average air temperature of 19.5 C light winds (cf. Wiersma and Piersma 1994).

^e Based on estimates of Poot and Piersma (1994).

^f This is the sum of the two foregoing rows.

^g For fat gains we assumed an energy equivalent of 40 kJ/g and a deposition efficiency of 0.85. For fat loss we assumed the same energy equivalent and 100% assimilation efficiency. Note that since the daily gains or losses are expressed in W, for daily totals of fat storage or loss to be derived, the values first have to be multiplied by the number of seconds per hour (3600) and the number of hours per day (24), and be divided by the energy equivalent of fat.

the next major staging site in southern Brazil (Lagoa do Peixe in the state of Rio Grande do Sul; see Harrington et al. 1986) would require approximately 36 g fat (computed from Gudmundsson et al. 1991:fig. 7). Given that Red Knots stay for periods of about 6–8 d at San Antonio Oeste (Fig. 3), this would require a refuelling rate of 4.5–6 g fat/d. (Note that in the northward migration seasons in recent years, field observations on temporal changes of the extent of breeding plumage and abdominal profile [cf. Wiersma and Piersma 1995] have confirmed the passage of several

different waves of birds [P. M. González, unpubl. data].) The rate of fat storage predicted by the optimistic scenario for an energy budget (Table 3) would allow for this refuelling period and flight distance, but the scenario based on the averages would not. Further work on body mass gains, activity budgets, food intake rates, and wind conditions during northward flight (see Piersma and Van de Sant 1992), along with studies on individually marked Red Knots to study individual performance, are needed to explore further the poorly known migration energy budgets.

It is clear that San Antonio Oeste provides an important refuelling area for northward migrating Red Knots, and that this importance is due to high densities of a suitable prey, the mussel *Brachidontes rodriguezi*, which are available on undisturbed areas of restinga. Future studies on the feeding ecology and food resources of Red Knots may show the extent to which there are inter-year variations in the use of the area in relation to variations in food abundance (cf. Beukema et al. 1993, Zwarts and Wanink 1993), explain the details of their local prey choice and feeding distribution, and indicate whether there are alternative local feeding areas to the ones used in 1992.

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